

ON THE STRUCTURE OF THE PALATE IN *DICYNODON*,  
AND ITS ALLIES.

BY R. BROOM, M.D., B.Sc.

(Read August 29, 1900.)

(Plate XXV.)

Though various accounts have been given of the structure of the palate in *Dicynodon* and its allies, it must be admitted that as regards many details of structure very little is known, and even where there is general agreement as to the structures there is much discrepancy in the interpretation of the elements.

Owen,\* in his "Reptiles of South Africa" and other papers, has shown the general arrangement of the bones in the roof of the mouth; but as regards the limits of the different bones he does not supply very definite information.

Huxley † made sections across the anterior part of an imperfect skull of *Ptychosiagum Murrayi*, and thereby revealed the presence of an extensive though delicate median osseous septum, which he regarded as an ethmo-vomerine septum. He gives fairly good figures of his sections, but his interpretation of the structure of the septum is altogether erroneous.

Lydekker, ‡ in the British Museum "Catalogue of Fossil Reptiles," gives a figure of the palate of *Dicynodon* with a determination of the elements.

The fullest account, however, of the *Anomodont* § palate is that given by Seeley || in 1889. He gives a figure of the palate of *Dicynodon*, and a description of the bones. Though Seeley's de-

\* R. Owen, "Cat. Foss. Rept. South Africa," 1876.

† T. H. Huxley, Quart. Journ. Geol. Soc., vol. xv., p. 654, and plate xxii., figs. 3-6.

‡ R. Lydekker, "Cat. Foss. Rept. and Amphib. Brit. Mus.," part iv., 1890, p. 18.

§ The term *Anomodontia* or *Anomodont* used throughout the paper is employed as by Cope, Baur, and Zittel to denote the order or sub-order of which *Dicynodon* is the type, and not as it is employed by Lydekker and Seeley for the large subclass of Reptiles with mammalian affinities.

|| H. G. Seeley, "On the *Anomodont* Reptilia and their Allies," Phil. Trans., 1889.

scription is fuller and more accurate than that of the earlier authors, we are still left in a state of much uncertainty on a number of points on which it is of great importance for the morphologist to have light.

While engaged in the study of the comparative anatomy of Jacobson's Organ I was led to the conclusion that the lacertilian so called "vomer" is not the homologue of the mammalian vomer, but of the "dumb-bell-shaped bone" in *Ornithorhynchus* and of the palatine process of the premaxillary in the higher mammals. For this element which is usually ankylosed with the premaxillary as its palatine process, but which remains distinct throughout life in *Ornithorhynchus*, and in the little cave bat, *Miniopterus schreibersii*, I proposed the name of Prevomer.\* To find further evidence in support of my position I naturally turned to the Theromorous reptiles as showing affinities with both the lizards and mammals. The examination of the beautiful skulls of *Gomphognathus* discovered by Seeley revealed that not only is there a well-developed true vomer, but that anteriorly are a pair of prevomers, situated exactly as are the palatine processes in the higher mammals but apparently quite distinct from the premaxillary.†

In the *Anomodont* skull the great development of the premaxillary renders the examination of the vomerine region difficult, and I found it impossible to get very satisfactory results from the British Museum specimens, though it soon became quite manifest that the median ridge on the posterior part of the hard palate which has been regarded by all previous writers, so far as I am aware, as the vomer, could not be the true vomer which undoubtedly is situated in the angle between the two anterior branches of the pterygoids.

Since returning to South Africa I have come across a number of specimens, the examination of which has enabled me to settle definitely almost all the details of the anatomy of the palate.

In *Dicynodon* and its near ally *Oudenodon* there is a well-developed bony roof to at least the anterior half of the mouth. On the anterior part of this bony roof or hard palate are two parallel longitudinal ridges, and in the posterior part is a well-developed median ridge. The structure of this hard palate has been a matter of some difference of opinion, as in the majority of the British Museum specimens the sutures are very indistinct. But while opinions have varied as to the extent of the premaxillary and maxillary elements, there has been a general agreement in regarding the median ridge as the vomer.

\* R. Broom, "On the Homology of the Palatine Process of the Mammalian Premaxillary," *Proc. Linn. Soc. N.S.W.*, 1895, p. 555.

† R. Broom, "On the Occurrence of an apparently distinct Prevomer in *Gomphognathus*," *Journ. Anat. and Phys.*, vol. xxxi., p. 277.

The examination of a beautifully weathered palate in the Port Elizabeth Museum, which I have elsewhere described as the type of *Oudenodon truncatus*,\* shows that almost the whole of the palatal surface of the hard palate is formed by the premaxillary, and a transverse fracture through the median ridge reveals that the ridge is, if not morphologically a part of the premaxillary, at least an element completely anchylosed to the premaxillary. Figure 3, Pl. XXV., represents semi-diagrammatically a transverse section through the median ridge of *Oudenodon*. It is here seen that though the maxillary has large palatal plates they are to a great extent overlapped by the premaxillary plates. Above the palate is seen the median internasal plate of the premaxillary. This median plate extends from the anterior part of premaxillary backwards as far as the palatal portion, and is closely articulated posteriorly with the large median plate of the true vomer. In *Dicynodon* the structure of the premaxillary, so far as I have been able to observe, is quite similar.

In *Ptychosiagum* † the general arrangement of parts is similar to that in the more normal genera, though the proportions differ somewhat. Figure 1 represents the palate of *Ptychosiagum*. Here as in *Dicynodon* and *Oudenodon* the palatal plates of the premaxillary overlap the plates of the maxillary and form the larger portion of the bony palate. The median ridge is much more conspicuous than in the less specialised genera, projecting very considerably from the rest of the palate. It passes backwards a short distance beyond the limit of the lateral palatal plates and articulates with the anterior end of the vomer by an interdigitating suture. Only a small portion of the maxillary shows on the palate between the premaxillary and the anterior part of the palatine. It forms a distinct though imperfect secondary palate, its inner edge not quite meeting the median ridge. Immediately behind the median ridge is seen the well-developed vomer.

Figure 2, Pl. XXV., represents a median section of the snout of *Ptychosiagum*, and shows very clearly the structure of the internasal septum. The internasal ridge of the premaxillary is very greatly developed, its depth being about equal to the antero-posterior measurement of the premaxillary. Immediately behind the large

\* R. Broom, "On Two New Species of Dicynodonts," Ann. South African Museum, vol. i., pt. 3, p. 455.

† As Owen's name *Ptychognathus* is preoccupied by Stimpson, 1858, for a Crustacean genus, I have adopted provisionally Lydekker's name *Ptychosiagum*, 1889. Cope had, however, described a species of this same genus in 1870 under the name of *Lystrosaurus frontosus*, and if Cope's name is not preoccupied it will take the place of Owen's name. When writing in the bush away from libraries it is impossible to decide on questions of nomenclature.



vertical plate of the premaxillary is situated the vomer, as an irregular triangular plate. It articulates with the premaxillary plate inferiorly by an interdigitating suture; but superiorly, the vomer divides into two delicate plates between which the premaxillary plate passes. Posteriorly the vomer articulates with the prespheroid clasping its anterior and inferior border. At its posterior and inferior angle the vomer divides to two small branches which pass outwards and backwards to meet the pterygoids. Above these branches the vomer for a short distance is quite separated from the prespheroid by an oval space.

Though both the premaxillary and the vomer form such large median plates, the plates are for the most part exceedingly thin, as is well shown by Huxley's sections. In figure 2 the letters AA, BB, and CC indicate approximately the positions of Huxley's three sections. His front section, AA, lies slightly above the palatal plate of the premaxillary, and shows the internasal plate of the premaxillary to be moderately thick in its anterior region. His next section, BB, passes through the palatine bone in its anterior and greatly developed region. The median plate is here formed of the premaxillary above and the vomer below, the premaxillary fitting into a deep cleft in the vomer. In the posterior of Huxley's sections the median plate is almost entirely formed by the vomer, only a very small portion of the premaxillary plate presenting above fitted into the cleft of the vomer. At its lower end the vomerine plate is seen to be cleft. Outside of the vomer the palatine and pterygoid are seen cut across—the lower being the pterygoid.

On each side of the vomer near its posterior border is developed a small lateral wing which articulates with the palatine and forms with it the posterior walls of the nasal passage. In figure 2 a dotted line indicates the position of the lateral wings.

The posterior part of the vomer is exceedingly well shown in more than one of the British Museum specimens, more especially in the imperfect skull which formed the type of Owen's *Ptychognathus boopis* (Spec. No. 36253) and in the skull which formed the type of *Cistecephalus chelydroides* (Spec. No. 47068), and it seems remarkable that there should have been any doubt as to its being the true vomer, more especially as in some mammals the posterior part of the vomer presents a strikingly similar appearance. Seeley,\* in describing the skull of *Dicynodon copei* [= according to Lydekker, *Ptychosiaugum Murrayi*, Huxley], suggests the possibility of this element being the vomer. He says: "In the constricted middle

\* H. G. Seeley, "On Anomodont Reptilia and their Allies," Phil. Trans., 1889, p. 241.

plate of the pterygoid is a long median vacuity, lanceolate behind, and tapering in front to a slender point. It is defined laterally by very slender plates, which converge inward and forward to form a single median plate, reaching forward to the maxillary region : and this plate may probably be identified as the vomer." In the same paper, however, he describes the almost identically similar structure in *Dicynodon* (*pardiceps* ?) as part of the pterygoid, and figures the median ridge of the premaxillary as the vomer.

The palatines in *Ptychosiagum* are fairly well-developed bones which form to a large extent the posterior and outer walls of the nasal passages. Posteriorly each palatine articulates with the lateral wing of the vomer, and along its inferior third it meets on its outer side the anterior spur of the pterygoid. From its articulation with the vomer the palatine is developed both in a lateral direction and anteriorly. The lateral wing passes outwards and upwards to meet the jugal. The anterior development passes slightly outwards, and then forwards, meeting and resting on the inner side of the maxillary and of the pterygoid. In this region the maxillary sends a short plate backwards, which in part lies on the palatine, but is mainly separated from it by the anterior spur of the pterygoid. Inside of the pterygoid spur and the maxillary the palatine is well developed anteriorly, and forms an imperfect secondary palate, articulating with the palatine plate of the maxillary. It does not, however, meet the vomer or the median ridge of the premaxillary.

The pterygoid requires but little description ; the posterior spur to the quadrate and the anterior development to the maxillary having been correctly described by Seeley. Though the median structure in front of the pterygoids is the vomer there are two small delicate plates which rise from the pterygoids and lie on the inner sides of the posterior branches of the vomer, forming in part the walls of the median vacuity. The bone with which the united pterygoids are articulated is evidently the basisphenoid, but the anterior continuation of the bone is possibly the presphenoid. I have been unable to detect a suture between the parts, but in *Dicynodon* there is a peculiarity in the arrangement of the fibres that suggests the probability of the two elements being present ankylosed together.

In *Dicynodon* and *Oudenodon* the structure of the palatines and pterygoids is very similar to that described in *Ptychosiagum*, the main differences being due to the fact that in *Ptychosiagum*, as in the Cetaceans, the nasal passages lie almost vertically, while in the less specialised types the passages pass as in land mammals in an antero-posterior direction.

In *Cistecephalus* the anterior part of the palate is unknown, but as the pterygoids, the vomer, and at least the posterior part of the palatines are constructed almost exactly as in *Ptychosiagum*, and as the rest of the skull, so far as known, is thoroughly *Dicynodont* in type, it is very unlikely that the anterior part of the palate differs appreciably from that in *Ptychosiagum*.

In *Endothiodon*, which forms the type of the other family of the *Anomodontia*, the palate, though closely agreeing with the *Dicynodont* type, presents a number of peculiarities. The main differences are due to the greater development of the maxillary, which bears a row of teeth, and the corresponding less development of the premaxillary. The premaxillary is, as in *Dicynodon*, edentulous. Its anterior palatal portion is moderately developed in *Cryptocynodon simus*, but is relatively smaller in *Endothiodon* (*Esoterodon*) *uniseriis*. The median ridge of the premaxillary is much more distinct than in *Dicynodon*, and though in none of the known specimens is there conclusive evidence that it is distinct from the premaxillary, there is certainly a strong suggestion of its being a prevomer. The vomer is very distinctly seen in the three known specimens immediately behind the median ridge—exactly as in *Dicynodont* type. In Seeley's figure of *Cryptocynodon*\* the division of the vomer from the anterior element is not very distinctly brought out, and from his description it is evident that he did not recognise the two elements as he speaks of the whole ridge, vomerine and premaxillary or prevomerine, as "presumably formed by the vomer." In the original specimen the anterior end of the true vomer is sharply defined from the premaxillary ridge, almost exactly as is the case in *Endothiodon bathystoma* and *E. uniseriis*. The palatines are formed on a very similar plan to that of *Dicynodon*. They articulate with the vomerine wings or lateral ridges, and form the posterior and upper walls of the nasal passages behind. Anteriorly they form an imperfect secondary palate, though a larger one than in *Dicynodon*. The hinder part of the palate is unknown, but presumably similar to that in *Dicynodon*.

The *Anomodont* palate, it will be observed, does not show a marked affinity with that in my Reptilian order, except the *Theriodontia* and the *Chelonia*; while as regards the vomer and palatines there is a distinct affinity with the Mammalian type. In almost all the known Reptilian orders the palate is formed essentially on the *Rhynchocephalian* type. In the *Chelonia* and the *Crocodylia* there are specialisations which greatly mask the ancestral type, and this is likewise the case with the *Theriodontia* and the sub-order *Anomodontia*.

\* H. G. Seeley, "On the *Therosuchia*," *Phil. Trans.*, vol. 185, B., 1894.



In the Cotylosauria, as exemplified by the American genus *Pariotichus*, and by the European and South African genera of presumably the same order, *Elginia*, *Pareiasaurus*, and *Procolophon*, the palate is made up of a pair of large, usually tooth-bearing pterygoids, a pair of small palatines and transpalatines, and a pair of large prevomers. The posterior nares lie by the sides of the prevomers, and there is no secondary palate formed.

In the Pelycosauria, as exemplified by the genus *Dimetrodon*, the general arrangements of the palatal elements is very similar to that in the Cotylosauria, except that the transpalatine is either lost, or, as suggested by Baur and Case,\* rudimentary. The posterior nares open by the sides of the prevomers and near the front of the palate.

Between the Pelycosauria and the Theriodontia, of which *Galesaurus* is the type, the gap is rather a wide one, and though a few possibly intermediate types are known, they are known so imperfectly that they are of comparatively little use in the tracing of the evolution of the palate. Though *Ælurosaurus* has always been regarded as a Theriodont and a close ally of *Galesaurus*, the palate, so far as known, is very dissimilar, and resembles considerably that of *Dimetrodon*. The posterior part of the skull is quite unknown. It may be noted, however, that the jugal or squamosal does not form a descending process, as shown in the figures of Owen, Lydekker, and Seeley, a calcareous incrustation having apparently been taken for bone. In the Theriodontia, as exemplified by *Galesaurus* and *Gomphognathus*, the posterior nares are carried far back by the formation of a secondary palate. In the Anomodontia we find the secondary palate in a rudimentary condition, the bony plates of the maxillaries and palatines not meeting but still forming a firm support for the soft, fibrous palate. It seems highly probable that true Theriodonts will be discovered with the palate in the same rudimentary condition as is found in the Anomodonts.

With the formation of a secondary palate a number of important changes have taken place. The element so important as a basal support of the skull in Labyrinthodonts and other Amphibians—the so-called “*parasphenoid*”—becomes in the large majority of Reptiles quite rudimentary. With the formation of a secondary palate, however, a new function is given to it, and it becomes developed as a median support for the palate. This median support is handed on through the Theriodontia to the Mammalia, and forms the mammalian Vomer. The large prevomers of the Cotylosauria and the Pelycosauria being, with the formation of a secondary palate, no

\* G. Baur and E. C. Case, “On the Morphology of the Skull of the Pelycosauria, &c.,” *Anat. Anz.*, 1897, vol. xiii., p. 109.

longer required as supports for the palatal roof, become much reduced, and are retained only as supports for the cartilage of Jacobson's Organ.

The stages by which the Theriodont secondary palate has been formed from a simple palate of the Dimetrodon type are apparently analogous to the steps by which the Crocodilian palate has been evolved from the simple palate of its Phytosaurus-like ancestor.

The Anomodont palate is probably a specialised modification of the primitive Theriodont type, where the Theriodont character is somewhat obscured by the great development of the premaxillary. Whether the prevomer is lost or anchylosed with the premaxillary present evidence does not show. Theoretically it seems not improbable that the prevomer is retained anchylosed with the premaxillary, and the condition in Endothiodon would seem to confirm this view. The direct evidence, however, is rather against this view, and it is quite likely that the prevomer is lost, as frequently happens in mammals, *e.g.*, Pteropus, Echidna, &c.

I can find no trace of a transpalatine element in any Anomodont skull, nor of an "infranasal" bone.

---

## PLATE XXV.

---

AA, BB, CC, approximate planes of Huxley's sections of the snout of *Ptychosiagum*; Ju, Jugal; Mx, Maxillary; Pa, Palatine; Pmx, Premaxillary; P.S., Presphenoid; Pt, Pterygoid; P.Vo., Prevomer; Vo, Vomer.

FIG. 1. Palate of *Ptychosiagum*.

- „ 2. Median section of snout of *Ptychosiagum*.
- „ 3. Section across Premaxillary in region of median ridge of *Oudenodon*.
- „ 4. Section near posterior part of Vomer in *Oudenodon*.
- „ 5. Palate of *Endothiodon* (*Esoterodon*) *uniseri* — partly restored.  
(Reduced.)